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River birds' response to hydrological extremes: New vulnerability index and conservation implications

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ABSTRACT

There is growing evidence that as a consequence of climate change the frequency of extreme hydrological events will increase. Predicting the impacts of these extreme events on ecological systems is a major research challenge. It is predicted that change in future river flows, characterised by greater occurrence of floods and droughts, will have profound impacts on aquatic invertebrate communities by removing sensitive species and restructuring food networks. However, it remains unclear how an increase in these hydrological extremes will impact on riparian communities and species at higher trophic levels. Here, we describe a new methodology that facilitates the integration of quantitative outputs of species' distribution models with the expert knowledge of conservation practitioners to produce a species' vulnerability index (SVI). Using our SVI framework, we assessed and ranked the vulnerability of 16 river bird species to a potential climate-induced shift in the frequency, duration and magnitude of flood and drought events. Vulnerability was associated primarily with ecological traits that restrict species to in-channel riverine habitat. Whilst the SVI was developed to assess species' vulnerability to hydrological extremes on rivers, it is equally applicable to other environmental domains as well as a range of avian and non-avian taxa. Furthermore, this original methodological approach provides researchers and managers with a valuable conservation tool that allows them to identify the species most vulnerable to climate change impacts and plan mitigation and adaptation strategies.

1. Introduction

There is increasingly robust evidence that global warming and the associated increase in climatic variability will lead to more extreme climatic events (Hansen et al., 2012; Min et al., 2011; Seneviratne et al., 2014). Given their potentially profound impacts, understanding the role of extremes in shaping ecological systems has gained increasing importance and momentum (Smith, 2011a,b). Climate change is predicted to result in the intensification of key processes in the water cycle such as precipitation, evaporation and runoff (Durack et al., 2012). As river flows are coupled closely to atmospheric drivers (Laizé and Hannah, 2010), shifts in the distribution of precipitation will result in modified hydrological regimes characterised by increasing trends in the frequency, duration and magnitude of hydrological extremes, including floods and droughts (Pall et al., 2011; Prudhomme et al., 2013).

River flow is regarded as the 'master variable' (Power et al., 1995) in riverine environments as flow not only structures physical habitats (e.g. channel width and stability), but also determines the physicochemical properties (e.g. water temperature, dissolved oxygen concentrations) of in-channel habitats which, in turn, regulate a range of environmental processes (e.g. production, nutrient retention) (Ward et al., 2002). Subtle changes in the spatio-temporal heterogeneity of river flows can determine the distribution and abundance of certain taxa (e.g. aquatic invertebrates, fish) (Bunn and Arthington, 2002), while extreme high and low flows can exclude sensitive species and restructure food webs by simplifying the network architecture and reducing species' richness at higher trophic levels (Ledger et al., 2012). Thus, an increase in climate-induced hydrological extremes is likely to have dramatic impacts on riverine biodiversity. Yet, incorporating extreme events into the experimental design of ecological studies remains a considerable challenge (Thompson et al., 2013).

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Variability in river flows influences the spatio-temporal distribution of riparian consumers such as river birds (Royan et al., 2013). Flooding influences the habitat occupancy (Reiley et al., 2013), abundance (Chiu et al., 2008), breeding success (Strasevicius et al., 2013), breeding timing (Arthur et al., 2012), and survival (Chiu et al., 2013) of river birds. Moreover, changes in the quality of foraging habitat can determine the timing of foraging activities (Cumming et al., 2012). The maintenance of unregulated (near-natural) riverine hydrological variability, including the occurrence of flooding and drought events, can be beneficial to river birds, with both diversity and abundance declining on rivers where anthropogenically-regulated, stable flow regimes exist (Kingsford et al., 2004). The impact of river regulation can be highest for those bird species (e.g. European pied flycatchers *Ficedula hypoleuca*) adapted to feeding on emergent aquatic invertebrates (Jonsson et al., 2012; Strasevicius et al., 2013). However, extreme flow events can also have dramatic negative impacts on river-obligate birds through marked shifts in surface flows (Hinojosa-Huerta et al., 2013).

Our understanding of the vulnerability of river bird communities to hydrological extremes is limited because of a failure to focus on multiple species' responses to a range of hydrological extremes across large geographical areas. This may partly be explained by the low probability of occurrence of hydrological extremes but also by the lack of conceptual frameworks for studying extremes, given that the description of an event as "extreme" is catchment-specific and depends on previous flow conditions (Smith, 2011a,b). Consequently, a study of this type may be best achieved using long-term, large-scale, multi-species data as these will facilitate the investigation of species' ecological responses to hydrological parameters across a range of 'extremes' (e.g. statistical quantiles) and across a range of ecosystems which vary in their sensitivity to hydrological extremes.

Two tools used regularly to evaluate the effects of climate change on biodiversity are: (1) species' distribution models (SDMs), which relate data on species' occurrence (Jones et al., 2013) or abundance (Renwick et al., 2012) to environmental drivers, and (2) assessments of species' sensitivity and exposure to climate change effects to determine the vulnerability of species to climate change (Davison et al., 2012). We combined aspects of both of these approaches to define a new methodological framework for the development of a species' vulnerability index (SVI) to hydrological extremes. River bird data from the British Trust for Ornithology's (BTO's) Waterways Breeding Bird Survey (WBBS) were combined with mean daily river flow data from the UK National River Flow Archive (NRFA) to investigate the vulnerability of 16 river bird species to a potential climate-induced increase in the frequency, duration and magnitude of hydrological extremes (floods and droughts) across 117 river locations. We used the IPCC (2012) statistical definition of an "extreme" as being a statistically rare event (i.e. events outside a defined percentile under current climate conditions) and investigated the relationship between species' abundance and flow parameters measured across a range of extremes (e.g. 95th, 90th and 75th percentiles for low flows and 5th, 10th and 25th percentiles for high flows).

Vulnerability to climate change impacts is comprised of two separate facets: sensitivity and exposure (Williams et al., 2008). Sensitivity is mediated by the resilience and adaptive capacity of the species, as determined by factors such as specific ecological traits (Williams et al., 2008). Exposure depends on the degree of buffering offered by species' occupied habitat and species' behaviour that reduce future exposure to the specific climate effects (Williams et al., 2008). Following the methodology of other SVIs (Furness and Tasker, 2000; Garthe and Huppop, 2004; Williams et al., 1995), we obtained exposure scores by providing relative numerical scores to a set of key qualitative questions. These scores were then combined with quantitative outputs from an ensemble of SDMs to provide a framework for assessing species' vulnerability. SVIs offer researchers and managers a valuable conservation tool that allows them to identify priority species for conservation action (Davison et al., 2012).

The specific objectives of this study were to:

1. Identify species of river birds most sensitive to changes in the variability of high (flood) and low (drought) river flows.
2. Combine quantitative analyses of species' sensitivity with assessments of species' exposure to a potential future increase in hydrological extremes in order to develop an index of species' vulnerability.
3. Identify priority riverine locations that support greater abundances of species of high vulnerability.

2. Methods

2.1. Data

River bird data were obtained from the BTO's WBBS: a large-scale annual survey of UK breeding birds on rivers and canals (canals were excluded from this study). Each survey location comprised a single river within a random 2×2 km tetrad that was stratified to target accessible locations across UK regions and provide extensive national coverage. The survey location represented the nearest waterway to a randomly selected point within the tetrad. The WBBS protocol requires two visits to the survey location during the birds' breeding season – one in early April to mid-May and the second in mid-May to late June. Each location comprised a number of continuous 500 m-long linear transects positioned along one bank beside the river. During both visits, observers recorded all birds within 100 m of the transects and noted the number of 500 m transects surveyed so that the total sampling effort was quantifiable (up to 10 transects in a row [5 km] could be surveyed).To determine the response variable (relative abundance), we pooled species' counts across all transects in the sample year and then used either the sum of counts for the first or second visit depending on which was higher. This count was then divided by the number of transects to ensure that that variability in abundance was not confounded by heterogeneity in sampling effort.

The procedure used to select WBBS survey locations for analyses was as follows. First, survey locations within 10 km of a river flow gauging station were selected. To ensure the relevance of flow variables to survey locations, gauging station-survey site pairings were not used where a major tributary inflow or anthropogenic barrier occurred between the gauging station and survey location. Survey locations with a minimum of four repeated visits were then selected as datasets that involve multiple visits to sample sites provide more reasonable estimations of species' occupancy and abundance by reducing bias associated with detection probability (Royle and Nichols, 2003). Survey data between 1998 and 2011 (inclusive) were used but excluding data from 2001 as few sites were surveyed due to the foot-and-mouth outbreak when access to rural areas was restricted by the UK Government. Lastly, for each bird species in turn, we then selected survey locations where a species was recorded in at least 80% of survey years. This reduced the likelihood of including sites that had been newly colonised or sites where populations were extirpated during the survey time series in the analyses (Oliver et al., 2012). This final criterion also served to remove false zeros, caused by sampling outside species' habitat range, from datasets as well as limiting overdispersion and associated model parameter and standard error bias (Zuur et al., 2012). In total, 117 WBBS survey locations were used (Fig. 1), although the number of sites varied between species.

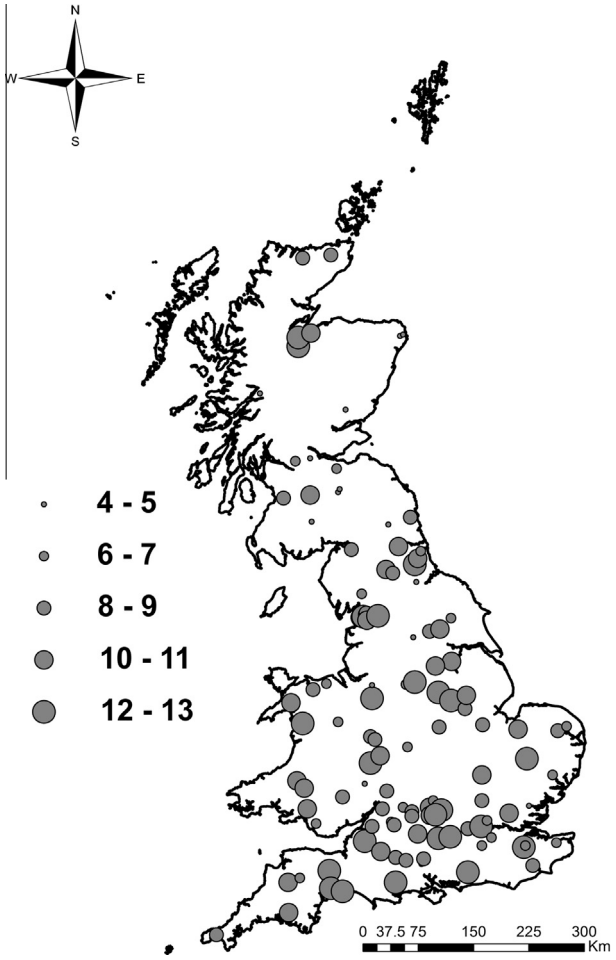

Fig. 1. Distribution of 117 WBBS survey locations across Great Britain. Graduated symbols illustrate differences in sampling effort (total number of 500 m transects).

For gauging stations with <10% missing values for any 1 year, we interpolated data gaps using long-term mean daily flows (Monk et al., 2008). Gauging stations with ⩾10% missing values were excluded from the analysis. The hydrological year in Great Britain runs from October to September (Bower et al., 2004) and bird data were paired with hydrological data from the associated hydrological year (e.g. bird data from spring 2010 were paired with hydrological indices calculated from daily flow data between 1st October 2009 and 30th September 2010). This meant flow variability was measured before, during and after the breeding seasons of focal avian taxa. This was preferable to calculating flow variables from a snapshot of the flow data (e.g. during the respective species' breeding seasons) as it allowed species' abundances to be related to long-term flow variability and its impact on the fluvial processes that create river habitats.

2.2. Modelling approach

To provide a quantitative measure of the sensitivity of river birds to hydrological conditions, for 16 river bird species we modelled the relationship between species' relative abundance and a range of hydrological parameters that quantify the three important facets of river flow variability (flow frequency, duration and magnitude) (Monk et al., 2007) for high (flood) and low (drought) flow conditions (Table 1). As significant collinearity existed between these flow parameters (typically $Rs > 0.7$), we modelled each parameter independently, resulting in an ensemble of 14 independent models for each species.

Table 1
Description of hydrological parameters used to characterise the main facets of flow variability (frequency, duration and magnitude) in species distribution models for 16 river bird species. Frequency and duration were characterised across a range of extremes defined using statistical percentiles (e.g. Q1 = 1st percentile).

Flow condition	Hydrological parameter
High flows	
Frequency	Number of flow events > Q1, Q10, Q25
Duration	Number of consecutive flow days > Q1, Q10, Q25
Magnitude	Maximum flow value/Q50
Low flows	
Frequency	Number of flow events < Q99, Q90, Q75
Duration	Number of consecutive flow days < Q99, Q90, Q75
Magnitude	Minimum flow value/Q50

The hierarchical nature of the WBBS dataset, involving repeated visits to the survey location, represents a considerable statistical challenge due to the lack of temporal independence between species' counts. Individual survey years will not contribute an entire degree of freedom to the analysis and conventional regression techniques underestimate the variance and standard errors (Vaughan et al., 2007). We used Generalized Estimating Equations (GEEs) (Liang and Zeger, 1986) to correct for this. GEEs accommodate correlated data by treating inter-cluster correlation as a problem parameter and by adjusting the confidence limits around regression parameters (Liang and Zeger, 1986). GEEs utilise a marginal model approach and, thus, model the expectation of the dependent variable as a function of the covariates by adjusting the covariance matrix of the estimated parameters to account for non-independence (Liang and Zeger, 1986). The marginal model approach is ideally suited to this study as it will account for collinearity in inter-annual river flow variability (Bower et al., 2004), which is considered as a 'nuisance parameter' that introduces undesirable noise to the data. Further notes on GEES can be found in Supplementary Appendices A1.1.

Models were fitted in version 1.1–6 of 'geepack' (Halekoh et al., 2006) in the statistical package *R*, specifying a Poisson error structure and a logarithmic link function. We also included a fully iterated jackknife variance estimator as the number of survey locations in the species' datasets was typically small (i.e. <30) (Halekoh et al., 2006), thereby reducing error in parameter estimation. As the inter-year correlation could be expected to decrease as time increases (Zorn, 2001), a first order autoregressive correlation structure was applied to all models. Where appropriate, square-root and logarithmic transformations were applied to parameters to satisfy assumptions of linearity.

2.3. Sensitivity scoring

For each independent model relating species' relative abundance to the flow parameters, the Wald statistic (z^2) was extracted and a Bayesian Information Criterion (BIC) value was calculated using the following equation (Raftery, 1995), where n = number of clusters (i.e. survey locations):

$$\mathrm{BIC} = z^2 - \log(n)$$

BIC values: <0 – indicate that there is no evidence to reject the null hypothesis; 0–2 – indicate a 'weak relationship'; 2–6 – indicate a 'positive relationship'; and >6 – indicate a 'strong relationship'. We assigned each BIC value a sensitivity score as follows:

1. BIC = 0–2.
2. BIC = 2.01–6.0.

3. BIC > 6.0.

As the frequency and distribution parameters were measured across a range of statistical extremes (see Table 1), the sensitivity scores assigned to these parameters were corrected to account for the parameter's likelihood of occurrence. This was achieved by dividing the sensitivity scores by the deviation from the mean, given a normal probability distribution, of the quantile associated with the parameter (i.e. sensitivity scores for: Q1 and Q99 parameters divided by 2.33 standard deviations (SDs); Q10 and Q90 parameters divided by 1.28 SDs; and for Q25 and Q75 parameters divided by 0.67 SDs). Total sensitivity scores were calculated for high (S_{high}) and low (S_{low}) flow conditions by summing the sensitivity scores for all parameters that quantify either high or low flow conditions, respectively. A total sensitivity score to a change in all flow conditions (S_{total}) was also calculated by summing sensitivity scores for both high and low flow conditions.

2.4. Exposure factors

We derived four factors from species' traits which all provided measures of species' relative exposure to climate change-driven flow alterations (Table 2). For instance, a species may be buffered from the full magnitude of flow alterations if it has little association with aquatic habitats for foraging or breeding and occurs across a broad range of habitats, if it has a broad foraging niche that enables it to take advantage of the increase in *r*-selected species that follows disturbance events (Ledger et al., 2012), or if it is highly dispersive and is at reduced risk of flow-induced mortality (O'Callaghan et al., 2013). All four factors were arranged on an exposure scale of 1 (i.e. low) to 3 (i.e. high) according to criteria detailed in Table 2. Initial factor scores were generated using comprehensive data published in del Hoyo et al. (1992–2013) and Cramp and Simmons (1977–1996) and were then independently moderated using the Delphi technique whereby scores were evaluated by a panel of six experts (expert profiles and scoring are in the Appendices: A1. 4 and Table A3) chosen according to their experience. When systematic and quantitative data are not readily available or easily applied to a methodological framework, this method has been favoured in many ecological studies (e.g. Davison et al., 2012; Furness and Tasker, 2000; Furness et al., 2012; Garthe and Huppop, 2004). Changes to the scores were made where three or more members of the panel suggested adjustments to the original scoring.

2.5. Vulnerability index

We produced an index for species' vulnerability to high flows (VI_{high}), low flows (VI_{low}) and a change in all flow conditions (VI_{total}) by developing a methodology similar to that of Garthe and Huppop (2004). First, the natural logarithm of the species' total sensitivity score (S_{total}), adding 1 to avoid undefined values, was multiplied by the average score for the four factors *A* to *D*. Each individual species' VI_{total} score was then expressed as a percentage of the maximum (11.49) and then divided into designated categories of vulnerability that ranged from low vulnerability to very high vulnerability.

$$VI = \sum_{species} (\ln(S_{total} + 1) * ((A * B * C * D/4))$$

2.6. Species' maps

We identified priority areas for species placed in the very high and high vulnerability categories by plotting the relative abundances of species across Great Britain using 509 WBBS survey locations. A surface of abundances was created using kriging, specifying a Gaussian semi-variogram structure. Kriging assigns values to un-surveyed locations using a weighted moving average technique, with the statistical relationship between spatially correlated points specified using the semi-variogram model (de Smith et al., 2013).

3. Results

3.1. Sensitivity scoring

Total sensitivity (S_{total}) ranged from 0 (grey heron *Ardea cinerea*) to 16.6 (common sandpiper *Actitis hypoleucos*), with high scores also for goosander (*Mergus merganser*) and mute swan (*Cygnus olor*) (Table 3; Fig. 2). The species that exhibited the most sensitivity to high flows (S_{high}) and low flows (S_{low}) were goosander, common sandpiper and mute swan (Table 3).

Species displayed very different responses to the hydrological parameters. We indicate in the Appendices (Table A1) where a specific increase in either the variability of high or low flows resulted in either a positive or negative shift in species' relative abundances. Some species displayed a positive relationship around either high or low flows. Typically, however, this was tempered by an aversion to an increase in variability at the other end of the flow spectrum. For instance, common sandpiper, cormorant (*Phalacrocorax carbo*), mute swan, reed bunting (*Emberiza schoeniclus*) and reed warbler (*Acrocephalus scirpaceus*) all showed an affinity to variability in low flows but an aversion to variability in high flows. However, some species showed an aversion to variability in both high and low flows (e.g. great crested grebe [*Podiceps cristatus*] and sand martin [*Riparia riparia*]).

Table 2
Criteria used to assign scores to exposure scores for four factors. See Section 2.4.

Exposure factor	Exposure score		
	1	2	3
Foraging habitat (A)	Tend to forage across a variety of aquatic, marine or terrestrial habitats with little association with specific aquatic/riparian habitats	Tend to forage in aquatic or riparian habitats	Tend to forage in specific aquatic habitats
Breeding habitat (B)	Tend to breed across a variety of aquatic, marine or terrestrial habitats with little association with specific aquatic/riparian habitats	Tend to breed in aquatic or riparian habitats	Tend to breed in specific aquatic habitats
Food specialisation (C)	Tend to forage across a variety of aquatic, marine or terrestrial habitats with little association with specific aquatic/riparian habitats	Tend to forage on aquatic taxa or taxa on marginal aquatic habitats such as gravel beds or mudflats	Tend to forage on aquatic taxa (e.g. fish, aquatic invertebrates and macrophytes)
Dispersal potential (D)	Nomadic or migratory	Non-migratory but can move large distances between habitat patches	Non-migratory, largely sedentary species with relatively small home ranges

Table 3
Species vulnerability index to a shift in flood and drought flow conditions for 16 river bird species.

Species	Locations	S_{high}	S_{low}	S_{total}	Foraging habitat	Breeding habitat	Food specialisation	Dispersal	$Exposure_{total}$	VI_{high}	VI_{low}	VI_{total}	VI_{total} (%)	Vulnerability
Goosander *Mergus merganser*	15	10.6	4.4	15	3	1	3	2	9	5.5	3.8	6.2	54.4	Very high
White-throated dipper *Cinclus cinclus*	28	5	0	5	3	3	3	3	12	5.4	0	5.4	46.7	High
Common sandpiper *Actitis hypoleucos*	12	6.8	9.8	16.6	2	2	2	1	7	3.6	4.2	5	43.6	High
Mute swan *Cygnus olor*	51	5.4	5.5	10.9	2	2	2	2	8	3.7	3.8	5	43.2	High
Great crested grebe *Podiceps cristatus*	10	3	1.7	4.7	3	3	3	2	11	3.8	2.8	4.8	41.6	High
Cormorant *Phalacrocorax carbo*	18	1.6	4.4	6	3	1	3	2	9	2.1	3.8	4.4	38.1	Moderate
Reed warbler *Acrocephalus scirpaceus*	16	3	4	7	2	3	2	1	8	2.8	3.2	4.2	36.2	Moderate
Common moorhen *Gallinula chloropus*	64	2.3	2.4	4.7	1	2	1	3	7	2.1	2.2	3.1	26.7	Moderate
Common kingfisher *Alcedo atthis*	18	2	0	2	3	2	3	3	11	3	0	3	26.3	Moderate
Grey wagtail Motacilla cinerea	44	1.2	1.8	3	2	2	2	2	8	1.6	2	2.8	24.1	Moderate
Sand martin *Riparia riparia*	13	0.8	4.3	5.1	2	2	1	1	6	0.9	2.5	2.7	23.6	Moderate
Reed bunting *Emberiza schoeniclus*	39	1.4	0.8	2.2	1	2	1	3	7	1.6	1	2	17.8	Low
Eurasian curlew *Numenius arquata*	21	0.4	3.7	4.1	1	1	1	1	4	0.4	1.6	1.6	14.3	Low
Northern lapwing *Vanellus vanellus*	21	3.7	0.4	4.1	1	1	1	1	4	1.6	0.4	1.6	14.3	Low
Eurasian coot *Fulica atra*	25	0	1.5	1.5	2	2	1	2	7	0	1.6	1.6	13.9	Low
Grey heron *Ardea cinerea*	65	0	0	0	1	1	3	2	7	0	0	0	0	Low

Vulnerability was described according to $\%VI_{total}$: 0 > 19.9 – Low; 20.0–39.9 – Moderate; 40.0–49.9 – High: ⩾50 – Very high.

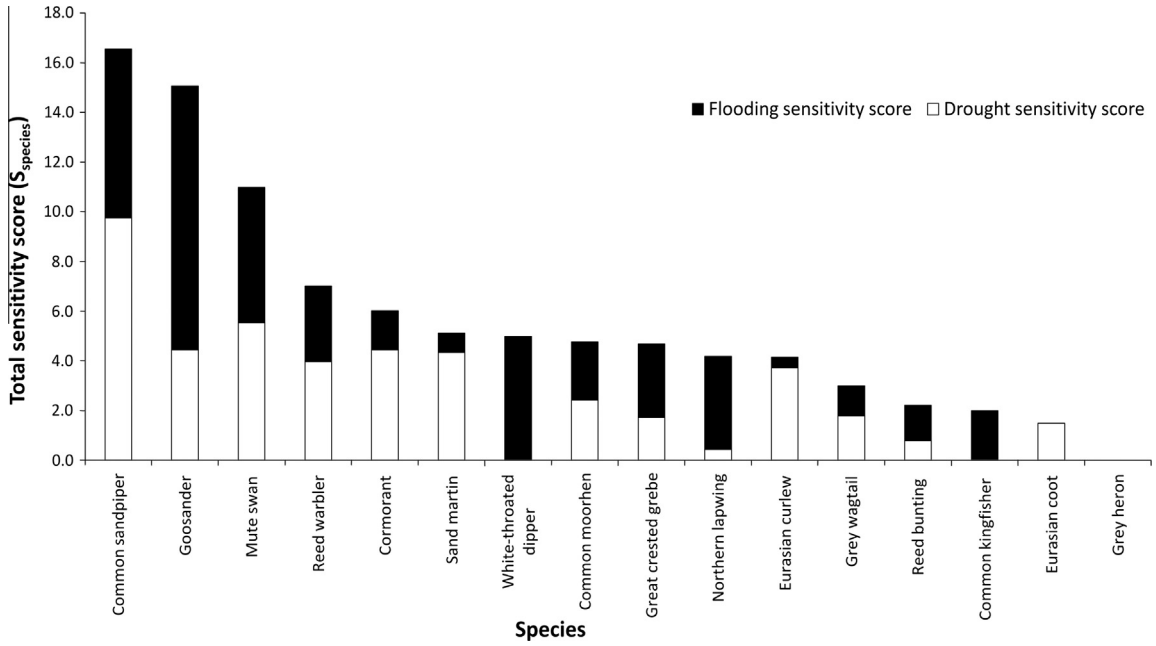

Fig. 2. Plot showing total sensitivity scores (S_{total}) for 16 species and the contribution to this by sensitivity to floods (S_{high}) and droughts (S_{low}).

3.2. Exposure and vulnerability scoring

The species judged to have the highest exposure to shifts in river flow ($Exposure_{total}$) were white-throated dipper (*Cinclus cinclus*), common kingfisher (*Alcedo atthis*) and great crested grebe, while goosander and cormorant also scored highly (Table 3). The species deemed to have the lowest exposure were Eurasian curlew (*Numenius arquata*) and northern lapwing (*Vanellus vanellus*).

The species with the overall highest total vulnerability (VI_{total}) was goosander, solely occupying the very high vulnerability category, with white-throated dipper, common sandpiper, mute swan and great crested grebe categorised as having high vulnerability

(Table 3). The least vulnerable species was grey heron. The species with the highest vulnerability to flooding (VI_{high}) were goosander and white-throated dipper and the species with the highest vulnerability to drought (VI_{low}) were common sandpiper, cormorant, goosander and mute swan (Table 3).

3.3. Species' maps

Priority regions for very high and high vulnerability species were identified by mapping species' abundances across Great Britain (Fig. 3). Relative abundances of goosander, white-throated dipper and common sandpiper were highest at riverine locations in upland regions of northern England, southern and northern Scotland and Wales, whereas those of mute swan and great crested grebe were highest at lowland riverine locations in south-east England.

4. Discussion

Ecologists have started to examine how climate extremes shape ecosystems (Smith, 2011a,b). This has been driven by an expectation that climate change will increase the intensity of extremes

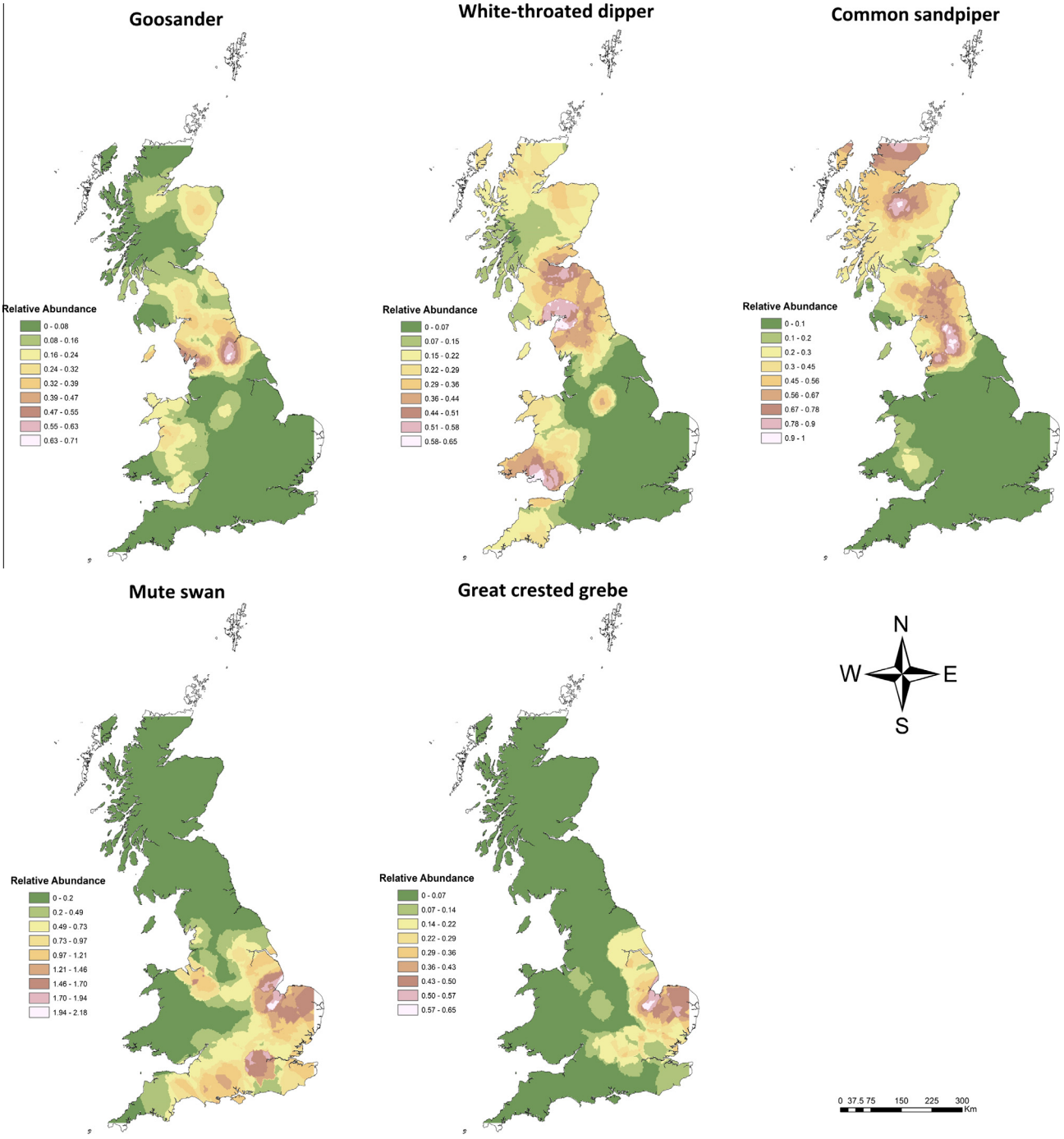

Fig. 3. Maps showing variation in the relative abundances of species identified as of very high and high vulnerability by the SVI (see Table 3 for further details) across Great Britain. Relative abundance was calculated as total counts divided by survey effort.

events (Hansen et al., 2012; Min et al., 2011; Seneviratne et al., 2014). Changes in climate extremes will have profound impacts on aquatic-riparian systems through shifts in flood and drought frequency, duration and magnitude (Pall et al., 2011; Prudhomme et al., 2013), creating novel flow regimes that will remove sensitive species and simplify the architecture of food web networks (Ledger et al., 2012). Whilst there is some evidence to suggest that this may have elevated impacts on species at higher trophic levels (Ledger et al., 2012), our understanding of the relationship between species' distributions and hydrological extremes is limited by a scarcity of large-scale studies that encapsulate both temporal and spatial variability in species' relationships with river flow. Here, we quantify the vulnerability of river bird species to a potential climate-driven shift in hydrological extremes by combining datasets from long-term national river bird surveys with river flow archives. We have demonstrated that the abundance of river birds is influenced by the occurrence of extreme river flows and that species are vulnerable to a potential future increase in occurrence of floods and droughts. Moreover, we highlight the importance of incorporating variability in extremes in climate change impact studies of ecological communities.

4.1. Vulnerable taxa

We were able to score and rank multiple taxa in accordance with their estimated vulnerability. By defining a methodology in which the outputs of correlative SDMs are combined with expert assessments of species' future exposure to climate change impacts, we quantified species' vulnerability to climate change in mainland Britain.

While some species such as goosander and white-throated dipper demonstrated an affinity to variability in high flows and common sandpiper to low flows, no species demonstrated an affinity to variability in both. As climate change is expected to alter the mean and variance of both high and low flows (Pall et al., 2011), this implies that all of the studied species with an association with one or more of the hydrological variables are vulnerable to some degree to climate-driven perturbations in river flow regimes. An arbitrary scheme was used to designate taxa into one of four vulnerability criteria, ranging from low vulnerability to very high vulnerability, based on final VI_{total} scores. Whilst the linear numerical criteria used to identify category cut-off points were simple, this ranking scheme facilitated the identification of priority species – this was one of the key aims of the study.

Using this approach, five species were identified as of high or very high vulnerability. These included species such as common sandpiper, goosander and white-throated dipper that are commonly associated with fast-flowing, upland rivers and streams in Great Britain (Fig. 3). Goosanders are found mainly on the wider stretches of the upper reaches of rivers during the breeding season (Gregory et al., 1997), while dippers are adapted to clear, fast-flowing upland streams where they feed on benthic macroinvertebrates and fish in riffles and pools (Tyler and Ormerod, 1994). It may have been expected that the positive relationship would exist between the abundance of these species and the parameters for high flow frequency and duration as observed. However, the strength of this relationship decreased as the high flow parameter became more extreme, suggesting that whilst some degree of variability in high flows is beneficial it is lost at higher flow events. This supports findings from studies of dipper activity budgets which demonstrated that time spent diving increases with rising flow discharge to a point but then dropped off as flow increases (D'amico and Hémery, 2007). This may be because the prevalence of favoured foraging microhabitats, such as riffles and pools, is reduced at extreme levels of high flow, but also because extreme high flows lead to mortality or increased dispersal amongst species at lower trophic levels in aquatic food webs, impacting the river birds' prey base (Chiu et al., 2008; Chiu et al., 2013).

In Great Britain, the common sandpiper breeds alongside fast-flowing, mainly upland rivers and typically forages at the water's edge on exposed riparian mudflats and gravel bars (Cramp and Simmons, 1977–1996; del Hoyo et al., 1992–2013). Abundance of this species was found to decrease with an increase in the frequency and duration of high flows whilst it increased with the frequency and duration of low flows. It is likely that increased variability in low flows increases the prevalence of exposed riparian foraging; however, in a similar manner to the white-throated dipper, the benefit of the increased variability in low flows decreased with the magnitude of the low flow event. Given that species' diversity in aquatic food webs and the contribution of larger-sized species to overall biomass decreases as the intensity of drought increases (Ledger et al., 2012), the abundance of riparian consumers may be negatively affected by this degradation of food web networks. This may have a greater impact on species such as the common sandpiper through a decline in aquatic-riparian food subsidies (Jonsson et al., 2012) than species such as the white-throated dipper that forages primarily on submerged aquatic prey.

A climate-induced increase in the frequency and duration of flooding may affect the foraging behaviour of these species, whereby birds will have to feed on a broader range of prey species or move to habitats peripheral to the main channel, such as smaller tributaries, where they are buffered from the full impacts of the flood, to find preferred prey species. This broadening of foraging niches would also increase the likelihood of intra- and inter-specific competition and perhaps impact foraging efficiency through patch depletion and decreased food handling time. If flooding were to occur during a sensitive period of the annual cycle, a shortage of prey could also limit breeding performance, for example, through phenological mismatch (Whitehouse et al., 2013) or carry-over effects (Harrison et al., 2011). These effects may be most profound for species with limited capacity for adaptive plasticity, which, in the short-term, might allow foraging and breeding efforts to be aligned with the locations and timings of peaks in resource availability (Charmantier et al., 2008). In the long-term, the costs on offspring productivity incurred from a mismatch between species' breeding behaviour and their prey will lower population viability (Visser et al., 2012). Whilst there is evidence from some species that genetic changes which alter the timings of seasonal events, such as breeding, have evolved in response to recent, rapid climate change (Bradshaw and Holzapfel, 2006), there is currently no consensus on how adaptive capacity can be best assessed quantitatively.

For lowland species, vulnerability was also associated commonly with species (such as the cormorant, great crested grebe and mute swan) that feed from the water surface on submerged prey or macrophytes. Species displayed negative relationships with high flow frequency and duration, suggesting that stability around high flows is favoured and they are negatively affected by flood events. Diving and surface swimming are likely to be the most energetically expensive activities for these species (Wood et al., 2013) which may not forage during extreme high flows when energetic investment in feeding may outweigh energy gain from ingested food (Taylor and O'Halloran, 2001; Wood et al., 2013). Foraging efficiency is likely to be severely compromised under conditions of elevated water velocity, depth and turbidity (Vilches et al., 2013).

Limited vulnerability was observed amongst species such as the Eurasian coot and grey heron that occupy a range of foraging and breeding habitats across the aquatic, riparian and terrestrial landscapes. The generalist foraging behaviour of some river bird species potentially buffers these species from the full impact of the predicted future change in floods and droughts. As predicted, low

vulnerability was also observed amongst species associated with habitats at greater distance from the main river channel.

Priority riverine locations which support greater relative abundances of very high and high vulnerability species were identified in upland regions of the north of England, southern and northern Scotland and Wales. Worryingly, these priority areas correspond with those regions predicted to have the largest percentage changes in river flow from climate change (Prudhomme et al. 2012), with large decreases in spring and summer flows and more variable autumn and winter flows predicted by a number of regional climate model scenarios. Given that previous investigations of climate change impacts on these species (e.g. goosander, white-throated dipper, common sandpiper) predict a gradual northward shift in range (Huntley et al., 2007), these species could increasingly become restricted to sub-optimal habitats where prey availability is reduced or more variable. It should be noted, however, that our application of kriging to identify priority river locations does not take into account river catchment boundaries or other physical patterns and involves interpolation across terrestrial features. Yet, this facilitates a valuable visual interpretation of how areas of high species' abundances correspond to the boundaries of river flow regimes (Bower et al., 2004) where climate change is predicted to have considerable impact on river flows.

4.2. Suitability of the vulnerability index

The species' vulnerability index presented here represents a novel and dynamic approach for assessing the impacts of potential future shifts in climate extremes. By combining long-term, national datasets on river bird distribution with river flow archives, the methodological framework presents robust quantitative assessments of species' relationships with hydrological extremes. However, by combining the outputs of SDMs with scores from expert judgements, the methodology also represents a very pragmatic approach to making rapid assessments and ranking the relative vulnerability of a range of species to potential climate change impacts. We hope that this approach will offer a potent conservation tool in the face of increased floods and droughts as predicted by climate modellers. Given the rapid rate at which climate change is occurring, conservation managers will have increasingly stretched resources which will necessitate targeted conservation action focussed on priority species and in priority geographical areas (Khamis et al. in press). Thus, a methodology that identifies hierarchical levels of vulnerability may allow conservationists to allocate management effort more effectively to the most vulnerable species.

The usefulness of an index is contingent upon the appropriate selection of the factors upon which it is constructed. Ideally, an index should be based on a combination of factors that explain the extent of species' distributions and regulate species' exposure to climate change impacts at microhabitat scales (Williams et al., 2008). In addition to the outputs of modelled distributions, here we used four factors which were assessed using subjective expert scoring. Whilst these four factors were qualitative in structure, ranking species relative to their perceived exposure, assessing these scores objectively and consistently using collected field data would have been inappropriate given the large variance within ecological traits across species. While it is possible that the SVI might have been improved by considering additional factors, this would have increased the amount of collinearity between factors which would have exaggerated the dichotomy in scoring between vulnerable and non-vulnerable species. The SVI also does not consider the size of species' range or species' conservation status, although the impacts of an increase in the intensity of floods and droughts may be more severe for species with small population size. However, the SVI was designed to assess the vulnerability of river birds that are, for the most part, ubiquitous across the British landscape. Moreover, we felt that the inclusion of conservation status as an additional factor might decrease the reliability of the results given that the parameters used to assess species' status (e.g. Birds of Conservation Concern 3 2009; Eaton et al., 2009) are not restricted to the riverine environment.

A further important consideration for any future application of this SVI is that the *z*-score, used in the calculation of the BIC, will be greater where n is large as the standard error of the parameter is reduced. There is, therefore, the potential in this study that the VI_{total} score of species recorded at a large number of survey sites (e.g. for mute swan) will be inflated. However, this is an unavoidable problem caused by converting coefficient values, which vary around the associated error, into a dimensionless index. In addition, the choice of n in calculating the *z*-score is also important. Raftery (1995) used the number of observations; however, here we used the number of survey locations as the observations within each location were not independent.

The SVI appears well-suited for assessing the vulnerability of river birds to hydrological extremes because the outputs showed clear differences between species and the vulnerability classifications were in broad agreement with knowledge on species' ecological traits – vulnerability was associated with traits that restrict species to in-channel riverine habitats and non-vulnerability was associated with more generalist strategies. Such findings are supported by other studies which have demonstrated clear relationships between the abundance and diversity of river birds and hydrological variability (Chiu et al., 2008; Kingsford et al., 2004). Secondly, sensitivity analyses showed that the SVI outputs were robust to small changes in both the sensitivity and exposure scores. Thirdly, the relative final vulnerability rankings assessed using the GEE approach were comparable to those of an alternative generalized linear mixed-effect model approach (see Table A2 in Appendices for a comparison of model outputs), indicating that the SVI framework is robust to the choice of modelling methodology used.

4.3. Concluding remarks: conservation implications

River bird populations have close relationships with river flows whereby natural variability and the occurrence of extreme high and low flows promotes species' diversity and regulates key life-history stages such as breeding as well as survival (Arthur et al., 2012; Cumming et al., 2012; Jonsson et al., 2012; Kingsford et al., 2004; Royan et al., 2013; Strasevicius et al., 2013). Species' responses to river flow parameters illustrate their vulnerability to a climate-induced shift in the frequency, duration and magnitude of hydrological extremes. Conservation efforts in an era of climatic uncertainty will increasingly rely on the careful targeting of valuable resources at priority species and regions (Khamis et al., in press). Therefore, practical methodological frameworks such as this will become increasingly valuable to applied conservation. Moreover, this study was made feasible by the availability of long-term and spatially broad annual bird survey data and daily river flow data, allowing species' distributions to be related to measures of hydrological extremes that are typically difficult to study due to their rarity and unpredictability. These data also allowed species' relationships to be placed in the context of previous exposure to the investigated parameter. This is extremely important given that the precise definition of an "extreme event" can be highly dependent upon the magnitude of previous flow events within a particular focal system (Smith, 2011a). The results discussed here emphasise the value and applicability of WBBS data and other repeated survey methodologies in the investigation of the impact of extreme events on ecological systems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.06.017.

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